

HYPOTHESIS TESTING WITH A COMPUTER MODEL FOR FORCE PRODUCTION IN MUSCLE

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Abstract —A computer model was designed based on the concept of *common drive* which suggests that motor units (group of muscle fibers and the single alpha-motoneuron that innervates them) in a muscle are controlled by a common input to the entire motoneuron pool. Where possible, the model utilized experimentally determined data and supplemented these with findings reported in the literature. It was validated by matching the simulated mean firing rates, power spectra, and compound muscle force outputs to that produced by data from the Tibialis Anterior muscle. The model was implemented using Matlab's ® SIMULINK ® tool. In this form, the model allows easy modification of parameters to allow for virtual experimentation that would otherwise be impossible with human or animal models. The developed model was used to evaluate a commonly used technique, spike-triggered averaging (STA), to estimate the twitch force of an individual motor unit. It was concluded that STA has the potential to produce valid estimates only at firing rates below 3 pulses per second which are physiologically unfeasible. Simulations suggest that the effects of common drive on reliable MU twitch estimation may not be as extensive as initially expected. Additionally, hypotheses regarding the effect of various mechanical characteristics under certain physiological paradigms such as hand dominance or fatigue on the electrical properties can be investigated using the model.

Keywords —Model, muscle, motor unit, spike-triggered averaging, hand-dominance

I. INTRODUCTION

Computer models provide a means to investigate physiological systems which are otherwise forbidding to experiment with either due to the difficulty in accessing or modifying defining parameters of the system. The present model was based on the model of Fuglevand et al. [7] which simulated isometric force from a model that predicted recruitment and firing times in a pool of motor units. It differed on a few points: The present model explicitly assumed a design that reflected the concept of common drive in that each motor unit received a common input- the common drive- and an input that was unique to that unit and not shared by others-the noise signal for the purposes of this model. The current model also differed from the Fuglevand model in various firing rate characteristics which were designed to reflect our observations in various but most specifically the Tibialis Anterior muscle [6]: the initial firing rate of a motor unit was dependent on its recruitment threshold; the excitation-firing rate profiles were not composed of a linear region followed by a saturation region, but were piecewise linear throughout the excitation range; the excitation-firing rate profile of each motor unit had a different shape. Furthermore, the pulse trains were estimated from the firing rate estimates by Integral Pulse Frequency Modulation rather than solving for interfiring intervals and hence firing times. The variability in interfiring intervals was achieved by the inclusion of the noise signal at the input rather than addition of noise to the interfiring intervals.

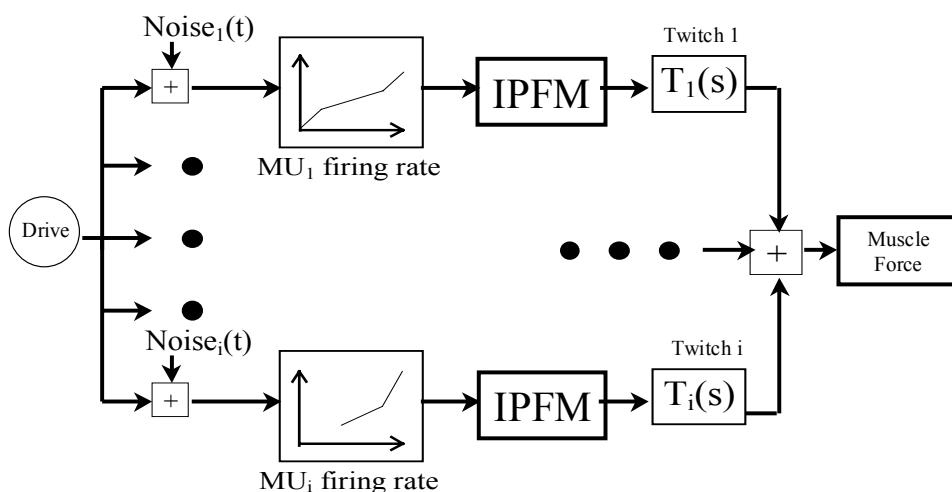


Figure 1 Model of force production in the muscle. Based on the concept of common drive, each motor unit receives the common input in addition to a noise signal. The drive is translated into a firing rate based on the characteristics of the motor unit, which are tightly associated with its rank. Integral Pulse Frequency Modulation stage generates the firing instances. The impulse response to the firings is the twitch waveform defining the force contribution of the motor unit. Muscle force is the summation of contributions of all motor units.

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II. THE MODEL

A. Underlying Theory

The observation that the firing rates of motor units fluctuate in unison with essentially no time delay between them has lead to the concept of *common drive* [4, 5]. This finding suggested that the CNS has evolved a relatively simple strategy for controlling motor units. Rather than controlling the activity of each motor unit separately, the CNS appears to control the excitation to the motoneuron pool. The common drive received by all the motor units in the pool gets translated into individual firing patterns for each motoneuron by the input/output characteristics of the motoneuron. Fluctuations in the common drive are reflected in concurrent fluctuations in the firing rate of motor units of the same pool.

Furthermore, it has been shown that various properties of a motor unit are interrelated [4, 6, 8]. For instance, Henneman's well-known size-principle states that smaller motoneurons and equivalently smaller motor units become active at lower levels of excitation [8]. Smaller motor units are also known to have lower twitch forces with longer relaxation times than larger motor units. Furthermore, motor units with lower recruitment thresholds, which can be assumed to be the smaller ones, maintain higher firing rates than those with higher recruitment thresholds. Yet another relationship exists between the rank or recruitment threshold of the motor unit and its firing rate response to increases in excitation [6]. In summary, the recruitment rank of the motor unit appears to define many of its firing (electrical) as well as twitch (mechanical) characteristics. These relationships have been exploited in defining and establishing the relationship between various characteristics of motor units in the present model.

B. Firing Rate Determination

Algorithms to produce the firing rates from the net drive for any particular MU were developed based on the force firing rate curves reported in [6]. In so doing, we assumed that the targeted force level represented the drive to the muscle. The equations reported in [6] along with curve fitting were used to generate closed-form representations of the drive-firing rate characteristics for each motor unit based on its recruitment rank. Figure 2 represents the distribution of the drive-firing rate profiles among motor units of the pool.

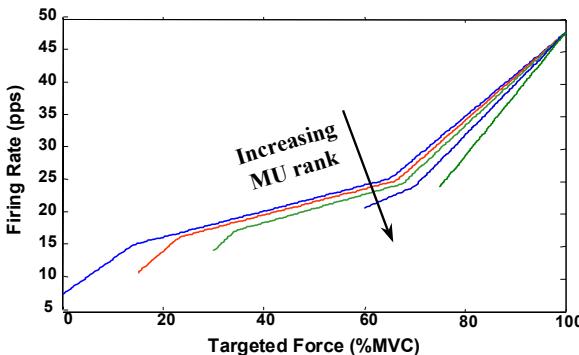


Figure 2. Force vs firing rate relationships assumed for motor units.

C. Firing Train Generation

Integral Pulse Frequency Modulation (IPFM) [2] was used to generate a firing train with a firing rate equal to the value determined by the drive-firing rate profile at the previous stage of the model. IPFM is essentially an integrate-and-fire system which integrates the input over time until a threshold (one for simplicity here) is reached. At this point, the integrator resets itself to zero and outputs a pulse of magnitude one. Hence, a lower input will result in firings to be spaced further apart compared to a larger input. The operation of the IPFM model is exemplified in Figure 3 for two different input levels.

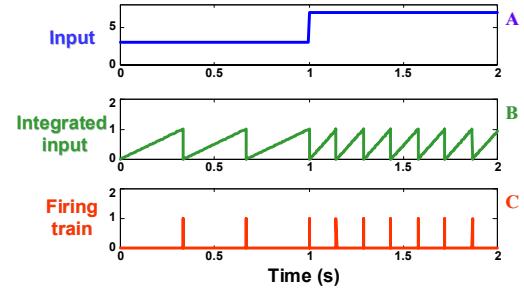


Figure 3. Generation of firing trains with Integral Pulse Frequency Model.

D. Generation of Motor Unit Twitches

In determining the shape of the force twitch the motor unit generates in response to a firing of the motoneuron, Fuglevand, et al. [7] developed the following equations after [9]:

$$f_i(t) = \frac{P_i * t}{T_i} * e^{-\frac{t}{T_i}},$$

where $P(i) = e^{b*i}$ and

$$T(i) = T_L * \left(\frac{1}{P_i} \right)^{\frac{1}{c}}.$$

Here, $f_i(t)$ is the twitch waveform of motor unit i . It depends on the parameters P_i and T_i , which represent the twitch peak force and contraction time, respectively. The coefficient b was set as $b = (\ln RP)/n$, where RP is the range of peak twitch forces and n is the number of MUs. T_L represents the longest duration contraction time and c was set to $c = \log_{RCT} RP$. RCT represents the range of contraction times for the pool of MUs. Contraction time is defined as the time from zero force to peak force [7]. These definitions and equations were adopted without change in the present work. Figure 4 displays the force twitches for various motor units in a pool of 150 motor units. In this simulation, a maximum contraction time (T_L) of 90 milliseconds, a contraction time range (RCT) of 3, and a peak twitch force range of 35 were assumed.

In defining the distribution of motor unit recruitment thresholds we again adopted the relationships described by [7]:

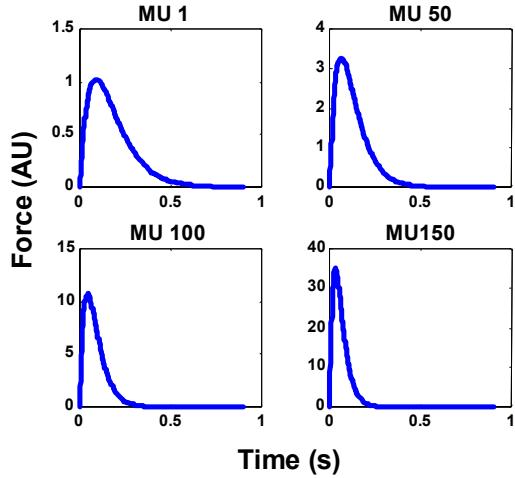


Figure 4. Twitch forces for motor units of various ranks.

$RT(i) = e^{a*i}$, where RT is the recruitment threshold and i is the MU number. The coefficient a establishes a range of recruitment thresholds. It was set to $a = (\ln RR)/n$, where RR is the maximum recruitment threshold for the pool and n is the total number of MUs being modeled [7]. A plot of recruitment threshold versus MU number is shown in Figure 5 for a pool of 150 motor units with a recruitment range up to 70 %MVC. These values were selected to emulate the Tibialis Anterior muscle on which the targeted force versus firing rate values were based.

III. VALIDATION OF THE MODEL

The model was validated using three methods. First, it was shown that the mean firing rates of MUs from the model matched the characteristics from those produced by real MUs. Secondly, the power spectrum densities of compound muscle force outputs from the model were compared to those of force outputs from human muscle. Thirdly, the output of the model when driven by a ramp input was verified. Although various parameters could be fine-tuned to improve the results, the outputs generated by the model were in general realistic. Figure 6 represents the force

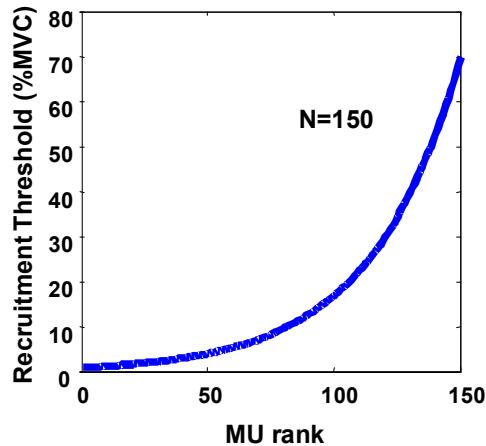


Figure 5. Distribution of motor units in a pool of 150 motor units with recruitment up to 70 % MVC.

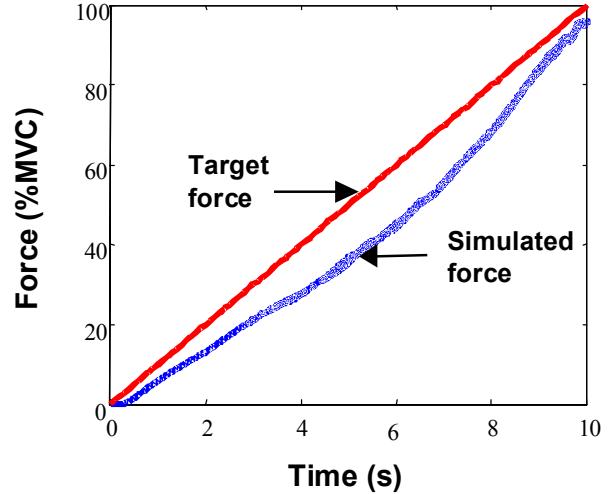


Figure 6. Validation of the model based on the force output produced.

output generated by the model (with parameters as defined for Figure 4) when driven with a linearly increasing input. The result approximates a linear increase that would be expected albeit with some deviation in the middle portion of the excitation range.

IV. SAMPLE APPLICATIONS

E. Spike-Triggered Averaging to Estimate Twitches

The model was first applied to the validation of the spike-triggered averaging (STA) [3, 10] technique to estimate the twitch force of individual motor units from the compound muscle force output. STA estimates the force-time characteristics of an individual twitch by summing and averaging multiple time frames aligned with the individual firings of the motor unit in question from the compound muscle force output. The underlying assumptions behind STA are that a motor unit's individual twitches do not fuse together, and the twitches of other motor units are uncorrelated with those of the motor unit in question. Fusion of twitches would hinder the contributions other than the single twitch to be averaged out since the next firing of the same motor unit would also fall in the averaged frames. Likewise, the correlation among motor unit firing patterns would keep the contributions of other units from falling at random instances within the frames taken with respect to the firings of the motor unit under investigation, hence prevent them from canceling out on the average.

We used the model discussed above to investigate how confining a) higher firing rates and b) correlation among the firings of motor units were. Figure 7 presents the effect of firing rate on parameters commonly used to characterize twitches: peak force, contraction time and half-relaxation time. Model parameters were the same as those for Figure 4. The motor units were driven independently (i.e., common drive was zero) in order to remove the effects of correlation on the estimates. It can be noted that even at firing rates that are too low to be physiologically viable, the estimation error reaches unacceptable levels.

The effects of correlation among motor unit firing patterns were investigated by varying the SNR (defined as the ratio of the

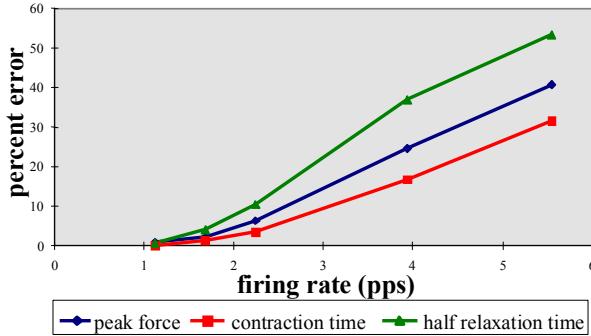


Figure 7. Effects of motor unit firing rate on of twitch force estimated by STA.

signal or common drive to noise). Figure 8 presents the estimation results for the three twitch parameters at SNR values of 1, 2, and infinite. The model parameters were the same as before. The drive was set at 5% MVC in order to minimize the effects of fusion. It can be noted that even at SNR values of 1, the twitch estimation becomes so noisy that the derivation of twitch parameters becomes a futile effort.

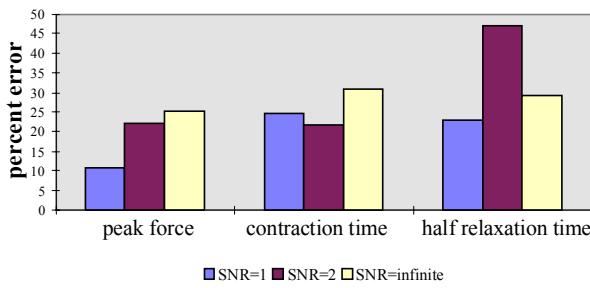


Figure 8. Effects of correlation among firing behavior on of twitch force estimated by STA.

F. Hand Dominance

The model was used to investigate the effects of hand dominance on the behavior of motor unit firing rates. In specific, the known differences among the dominant and nondominant muscles were implemented and simulations were run to determine what could be concluded about the firing rates or drive to the pool. Figure 9 presents the results of simulations run to represent the dominant and nondominant muscles. More explicitly, although slower and smaller motor units were assumed for the dominant side to represent the shift toward more Type I fibers, their recruitment range was narrower to parallel experimental findings [1]. The number of motor units were the same in both cases. It can be seen from Figure 9 that given these parameters, for the same drive, the dominant muscle would overshoot the target if it did not generate lower firing rates than the nondominant side as seen in experimental data [1]. It remains to be determined whether the lower firing rates are effected via a lower excitation or changes in the drive-firing rate characteristics.

V. CONCLUSIONS

The implemented model can be useful in studying various techniques or physiological paradigms. It goes without saying that the model is based on a multitude of assumptions and the results can be as valid as the assumptions made. In general, the

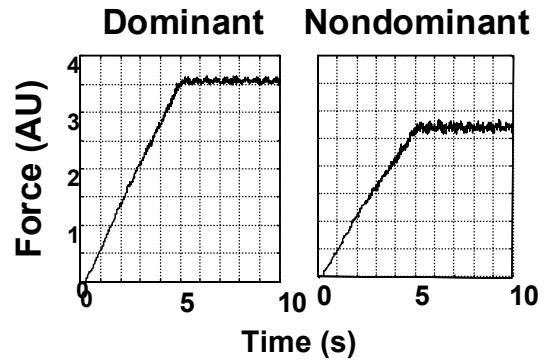


Figure 8. Effects of correlation among firing behavior on of twitch force estimated by STA.

strength of modeling studies lies in not proving hypotheses but disproving unlikely cases, and investigating the overall consequence of paradigms with conflicting effects, such as fatigue which causes a decrease in twitch amplitude while increasing twitch duration. The availability of more detailed physiological information will improve the model, as will the inclusion of factors such as the nonlinear summation of twitches and time-dependence in the model.

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